COMPARATIVE ANATOMY OF LEAVES FROM SPECIES IN TWO HABITATS AROUND SYDNEY.

By Gladys Carey, M.Sc.

(Six Text-figures.)

[Read 30th November, 1938.]

This anatomical study was undertaken in the hope that it might throw some light on the morphology of xerophytes, perhaps revealing some characteristic of stomata or venation which would be distinctive for the plants of dry habitats. The results indicate that certain features of the vascular system do depend on the habitat, but the frequency of stomata seems independent of it. However, since data on stomatal frequencies have been published for plants in other climates (Salisbury, 1927; Wood, 1934), it is useful to record here some data on stomata obtained for plants in the environs of Sydney, New South Wales.

In the course of this work an examination was made of the structure of leaves from trees and shrubs in two distinct habitats, namely (*a*) sandstone ridges and slopes, bearing sclerophylls on the exposed heights and more mesic types on the lower slopes towards the valleys, and (*b*) valleys of shale supporting mesophytic rain-forest. Particular attention was paid to the nature of the stomata and venation, the two characters most likely to have functional importance. Apart from this special emphasis, several observations resulting from the more general study seem worthy of note. These are set out in the following paragraphs.

Cuticle.—It has been a recognized fact for some time that thickness of the cuticle varies with light-intensity, so that often plants in sparsely populated, exposed communities exhibit a greater development of cutin. However, there is considerable generic variation, some plants showing a greater facility for cutin-production than others. For example, in *Angophora cordifolia* on the lower surface of the leaf, the cuticle occurs as irregular furrows and folds which completely obscure the stomata in surface view (Text-fig. 1*a*). In *Banksia spinulosa* and *Epacris microphylla* in similar habitats, the cuticle, though thick, is devoid of ridges.

Thickness of leaf.—Although within any one species the percentage of thickness occupied by palisade tissue is controlled by light, there is between species a considerable variation in the absolute thickness of the leaves, irrespective of habitat. Among sclerophylls, there are leaves such as those of *Lomatia silaifolia* (*0·5 mm. in thickness, bilateral; Text-figure 5*c*) and *Isopogon anemonifolius* (0·66 mm., isobilateral), but in the same habitat there are thin leaves as seen in *Epacris microphylla* (0·25 mm., Text-figure 5*f*) and *Banksia spinulosa* (0·25 mm.). Similarly fluctuations are found among the rain-forest types. In *Eugenia Smithii* (0·36 mm.) and *Doryphora sassafras* (0·35 mm., Text-figure 5*b*), the leaves are thicker than those found in *Palmeria scandens* (0·23 mm.) and *Claoxylon australe* (0·23 mm., Text-figure 5*a*).

---

* These figures are the average of 50 counts, 5 on each of 10 leaves, representing at least 5 plants.

Sclereids.—Branched sclereids are formed in the mesophyll of the leaves of some genera. The most striking development of these cells among the leaves examined is shown in *Hakea saligna*, a lanceolate leaf, in which the palisade tissue is penetrated by branching sclereids extending from the epidermis to the spongy mesophyll. These cells are so extensive and numerous that they form, as seen from surface view, an interlocking system on both sides of the leaf (Text-figure 2); while in *H. gibbosa*, an acicular leaf, the sclereids are far fewer and dumb-bell shaped. Another genus which exhibits this feature is *Isopogon*. In *I. anemonifolius* branching sclereids are abundant in the spongy mesophyll, some projecting into the palisade; they are present also in *I. anethifolius*, but far fewer in number. The leaves of *Lomatia* are strengthened by these cells, occurring in both the rain-forest type, *L. Fraseri*, and the sclerophyll type, *L. silaifolia*.

The extent and nature of the cells in the bundle-sheath vary in the different genera. This will be discussed later in connection with the investigation of vascular tissue.

Morphology of Stomata.—Among the plants used in the determination of stomatal indices, there is wide variation in stomatal type. A description of the morphology of some stomata as seen (*a*) in section, (*b*) in surface view, will perhaps add emphasis to the conclusions reached.

(*a*) *In transverse section.* Two of the more extreme types of sunken stomata are shown in the genera *Hakea* and *Eucalyptus*. In *Hakea gibbosa* the guard
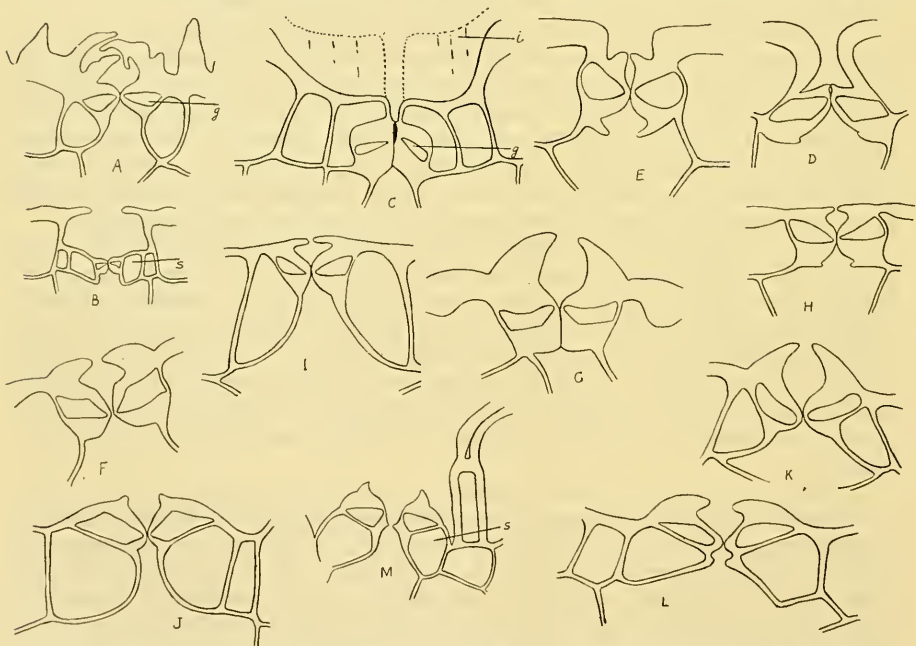
Text-figure 1.—The stomata shown in figures 1*a*-1*m* are freehand sketches; accordingly the magnifications do not allow comparison of size between the individual sketches.
a, *Angophora cordifolia* (G = guard cell); *b*, *Hakea gibbosa* (S = subsidiary cell); *c*, *Bossiaea scolopendria* (I = incrustation); *d*, *Gompholobium latifolium*; *e*, *Pultenaea stipularis*; *f*, *Isopogon anemonifolius*; *g*, *Hemigenia purpurea*; *h*, *Dodonaea triquetra*; *i*, *Ceratopetalum apetalum*; *j*, *Palmeria scandens*; *k*, *Doryphora sassafras*; *l*, *Lomatia Fraseri*; *m*, *Banksia spinulosa* (S = stalk cell).

cells are reduced in size and are held at the centre of the base of an extremely large air-cavity formed by over-arching of the cuticle, by several small epidermal cells (Text-figure 1*b*). These in surface view are not in focus with the larger interstomatal epidermal cells, thus making an accurate count of the total number of epidermal cells per unit area extremely difficult. In *Eucalyptus haemastoma*, the guard cells are well below the leaf-surface, although situated in the plane of the outer limit of the epidermal cell-cavities. This is due to the thickening of the outer walls of the epidermal cells and to a great thickness of cutin. An unusual type of stoma is found in the cladode of *Bossiaea scolopendria*; it lies at the base of a depression four cells wide and is protected by a flaky, colourless incrustation on the surface. The walls of the guard cells are exceptionally thick and can be seen in surface view only by focusing through the adjoining epidermal cells, which arch over them (Text-fig. 1*c*). Another type of depressed stoma is characteristic of *Gompholobium latifolium*, where the guard cells lie at the bottom of an air-chamber formed by the walls of the adjoining cells (Text-fig. 1*d*). A somewhat similar stoma is found in *Pultenaea stipularis* (Text-fig. 1*e*).

The sunken stoma is not, however, a feature of all sandstone plants. Quite a number show guard cells on the level of the epidermal cells, with the cuticle slightly arched, e.g., *Isopogon anemonifolius* (Text-fig. 1*f*), *Persoonia*, *Leptospermum* and *Hemigenia purpurea* (Text-fig. 1*g*). Similar stomata are of common occurrence among rain-forest species, e.g., *Dodonaea triquetra* (Text-fig. 1*h*), *Trochocarpa laurina*, *Synoum glandulosum*. In *Ceratopetalum apetalum*, on the other hand (Text-fig. 1*i*), the only unusual feature is the extreme difference in size between the guard cells and the adjoining epidermal cells.

In addition to the above types there are those with slightly raised stomata, e.g., in the rain-forest: *Palmeria scandens* (Text-fig. 1*j*), *Claoxylon australe*, *Doryphora sassafras* (Text-fig. 1*k*). On the sandstone this type of stoma on a glabrous leaf is most nearly approached in *Angophora cordifolia*, which bears guard cells level with the outer limit of the epidermis but protected by a series of overlapping arches of cuticle (Text-fig. 1*a*). Raised stomata on tomentose leaves are not infrequently found. For instance, in the recurved leaf of *Banksia spinulosa*, among the woolly unicellular hairs are guard cells raised above the general level of the epidermis by "stalk cells" (Text-fig. 1*m*). This type of stoma is mentioned by McLuckie and Petrie (1927). Similar stomata are found on the recurved leaves of *Lambertia formosa* and *Helichrysum diosmifolium*.

Thus it would seem that the position of the guard cells in relation to epidermis is not a sure guide to the nature of the habitat of the plant except perhaps in extreme cases. This has been demonstrated by Cannon also (1924) in plants of the arid regions of South Africa.

(*b*) *In surface view*.—An examination of surface sections of these leaves shows that for each genus there is a specific arrangement of the epidermal cells about the stomata. This can most readily be demonstrated by the observation of several text-figures. Text-figures 3*a* and 3*b* show the lower epidermis of two species of *Lomatia*, *L. silaifolia* from the sandstone and *L. Fraseri* from the rain-forest. The similarity of arrangement is self evident. Again, Text-figures 3*c* and 3*d* indicate the close agreement between cells of *Pultenaea elliptica* and those of *P. stipularis*.

The size of the epidermal cells depends upon the interaction of environment and heredity. This is illustrated by the fact that small and large cells are found among the species of plants in both habitats. *Sloanea australis*, a large-leaved member of the rain-forest flora, may have as many as 3,275 cells per
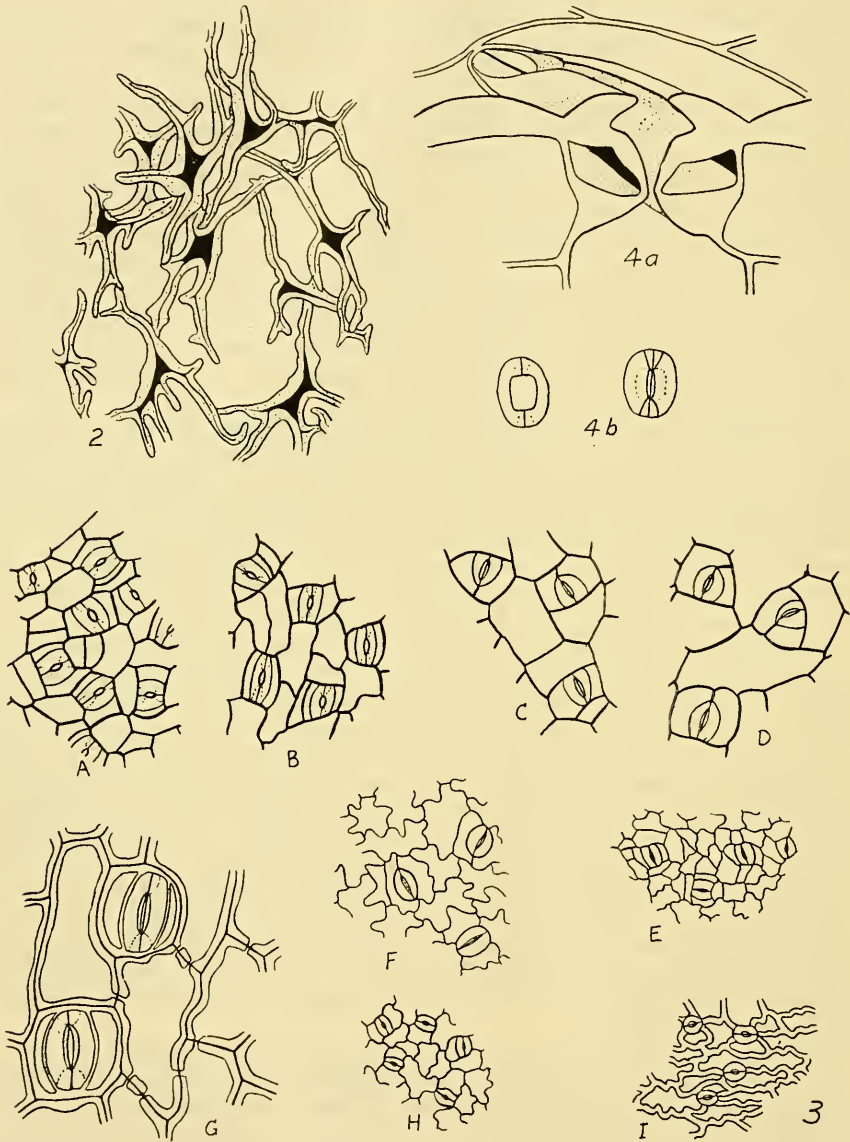
Text-figure 2.—Branching sclereids of *Hakea saligna* as seen in surface view of leaf. (× 150.)

Text-figure 3.—Surface view of the epidermal cells and stomata on the lower side of the leaf of: *a, Lomatia silaifolia*; *b, Lomatia Fraseri*; *c, Pultenaea elliptica*; *d, Pultenaea stipularis*; *e, Sloanea australis*; *f, Claoxylon australe*; *g, Persoonia salicina*; *h, Rhodamnia trinervia*; *i, Lysinema pungens*. (× 150.)

Text-figure 4.—*a,* A reconstruction of a half stoma of *Isopogon anemonifolius* (freehand); *b,* Surface view of stoma of *Isopogon anemonifolius* at two depths of focus (freehand).

square millimetre (Text-fig. 3*e*) on the lower surface, *Ceratopetalum apetalum*, 3,131 per square millimetre; while other members of the same community, such as *Claoxylon australe*, have as few as 749 per square millimetre (Text-fig. 3*f*) and *Rhipogonum album*, 611 per square millimetre. In the sclerophyll forest the variation is just as marked, in fact it so happens that the largest epidermal cells examined belonged to genera of this habitat. This is clearly indicated by the counts in leaves of *Persoonia*, which show an average of 208 cells per square millimetre in *P. pinifolia*; and of 127 and 133 per square millimetre on the upper and lower sides respectively in *P. salicina* (Text-fig. 3*g*). Small numbers are also found in species of *Pultenaea*, e.g., *P. stipularis* has an average of 395 per square millimetre and *P. elliptica* of 510 per square millimetre (Text-figs. 3*c* and 3*d*), while, on the other hand, *Lomatia silaifolia* may have as many as 1,675 per square millimetre.

The walls of the epidermal cells on both surfaces of the leaves of most rain-forest species exhibit, to a greater or less degree, convolutions or waviness of outline, as shown in *Claoxylon australe* (Text-fig. 3*f*), *Trochocarpa laurina*, *Rhodamnia trinervia* (Text-fig. 3*h*). An exception occurs in *Ceratopetalum apetalum* where this feature is absent altogether. In spite of the general nature of this feature among rain-forest plants, it is not exclusive to them; all that may be said is that, while apparently widespread in such habitats, it appears to be the exception rather than the rule among plants of sclerophyll forests. This does not preclude the influence of light on the character of these walls in any one species and it is interesting to note that, though the walls of the epidermal cells in *Lomatia silaifolia* are straight, those of *L. Fraseri* in the more shaded habitat of the rain-forest are wavy in outline (Text-figs. 3*a* and 3*b*). *Bauera rubioides* growing on the sandstone slopes and in the valleys shows this feature strongly, but it is just as pronounced in the leaves of *Epacris microphylla*, *Lysinema pungens* and *Persoonia salicina* (Text-figs. 3*i* and 3*g*), on the exposed sandstone ridges.

The structure of the stomata as seen from above requires no comment except in the case of that occurring in the Proteaceae, as seen, for example, in *Lomatia, Isopogon, Hakea* and *Persoonia*. In these the deposition of cutin seems to be heaviest about the pore and least about the junction of the guard cells, where it flattens out into two elliptical-shaped areas through which the contents of the guard cells can be readily seen. An attempt has been made in Text-figure 4*a* to reconstruct a half stoma in the solid, from a transverse section and surface sections at various depths of focus (Text-fig. 4*b*). The width of the air-cavity at the top of the stoma is variable. It is widest in genera such as *Persoonia* and *Lambertia*, and narrowest in types such as *Lomatia* and *Isopogon*.

The size of the stomata seems to be a hereditary factor on which the environment in each individual species exerts an influence, some species being more plastic than others. This is deduced from the fact that all sizes of stomata are found in both habitats, some of the largest belonging to the xerophytes. The semi-succulent *Persoonia* has stomata of unusual size, far larger than any other examined (Text-fig. 3*g*). The average long diameter of stomata of *Hakea gibbosa* (as determined from ten readings) measures 0·035 mm., those of *Eucalyptus haemastoma*, 0·038 mm.; while in the more humid, denser habitat the stomata of *Doryphora sassafras* are on the average 0·039 mm. in length, those of *Drimys insipida*, 0·034 mm. So there seems to be no significant difference in stomatal size among the different genera.

Stomatal Index.—In addition to the above general survey, counts were made of the epidermal cells and stomata in the same areas from which the stomatal
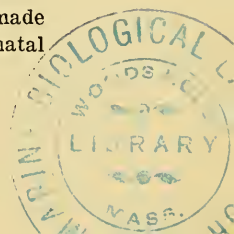
indices were determined. The field used was a square whose side measures 0·31 millimetre, for it was found that with a larger field accurate counting of smaller cells was almost impossible. The surface section used was taken in each case close to the middle of the leaf, in the wider leaves closer to the midrib than to the outer margin. Two branches were collected from any one plant and a leaf taken from each. The original plan was to take ten plants from several different areas, making twenty determinations in all for each species. However, this plan was not strictly adhered to, so that in some cases fewer determinations have been made. To summarize the results, the averages were obtained and their standard deviations (σ) calculated (Table 1). In this, the stomatal frequencies are included also, although it is realized from the method of sampling and the small number of counts that these figures cannot be taken as decisive; they give merely some idea of the order of frequency.

The species selected were trees and shrubs showing wide variation in height and leaf-form. In the sandstone sclerophyll forest were selected low-growing shrubs (e.g., *Platylobium formosum, Epacris microphylla*), taller shrubs (e.g., *Lambertia formosa, Gompholobium latifolium*) and trees (e.g., *Banksia spinulosa, Eucalyptus haemastoma*). Similarly in the rain-forest, low shrubs (e.g., *Rhodamnia trinervia, Drimys insipida*), tall shrubs (e.g., *Dodonaea triquetra, Lomatia Fraseri*) and trees (e.g., *Palmeria scandens, Doryphora sassafras*). These plants also exhibit divergence in leaf-form, ranging from small closely-set leaves (*Lysinema pungens*) to broad, well-spaced leaves (*Persoonia salicina, Angophora cordifolia*) and include dissected laminae (*Isopogon*), terete leaves (*Hakea gibbosa, Hemigenia purpurea*), narrow recurved leaves (*Banksia spinulosa*) and cladodes (*Bossiaea scolopendria*). In the rain-forest the variation includes the comparatively narrow leaves of *Lomatia Fraseri* and *Drimys insipida*, with gradations to the very broad leaves of *Sloanea australe* and *Rhipogonum album*.

In Table 1 it will be noted that in one instance, namely for species of *Pultenaea*, the stomata are found only on the upper side of the leaf. This is associated with the position of the leaves on the stem, for they are crowded together at an acute angle so that the under surface is the most exposed. This unusual position of the stomata is attended by the presence of one or two layers of colourless cells derived from the lower epidermis and separating it from the mesophyll in *P. elliptica* and similarly derived tannin cells in the same position in *P. stipularis*. Owing to the extreme difficulty in dealing with xeromorphic tomentose leaves which, if narrow (e.g., *Banksia ericifolia*), are often recurved; and if wide (e.g., *Banksia serrata, B. latifolia*), are depressed between the veins, stomatal counts are given for such a type only in one instance, namely, *Lambertia formosa*.

Salisbury (1927), in a paper on stomatal frequencies of British plants, introduced the concept of *stomatal index** for a number of plants from various habitats, from which he deduced "that high humidity tends to reduce the proportion of stomata found and aquatics would appear to have low stomatal indices". This is not, as a matter of fact, borne out by statistical analysis of Salisbury's data (Table 2), but it is noteworthy that there is a statistically significant difference between the stomatal indices of British woodland plants and those of the species investigated from the New South Wales rain-forest. The difference between the stomatal indices of British woodland plants and New South Wales sclerophyll forest types, is not so marked owing to the higher standard deviation in the latter.

---

* i.e., the percentage of epidermal cells which are stomata.

TABLE 1.

Stomatal frequencies, stomatal indices and percentage areas of leaf surface occupied by vascular tissue.
Sclerophyll Forest
on sandstone ridges and slopes.

Plant.	Type of Leaf.	S.F.u.	S.F.l.	S.I.u.	σ Mean. S.I.u.	S.I.l.	σ Mean. S.I.l.	V.B.	σ Mean. V.B.
Banksia spinulosa	narrow, recurved	—	—	—	—	—	—	52	1·66
Hakea gibbosa	terete	73	73†	7·1	0·92	7·1	0·93	—	—
Hakea saligna	lanceolate	(f)	94	—	—	7·4	1·14	—	—
Isopogon anemonifolius	dissected, flat	187	125	12·9	1·10	10·5	1·28	42	6·46
Isopogon anethifolius	dissected, terete	104	77	10·8	1·59	9·4	1·56	—	—
Lomatia silaifolia	2-3 pinnate	—	273	—	—	17·3	1·46	43	4·43
Lambertia formosa	narrow, linear, recurved	—	293	—	—	14·7	1·27	45	4·00
Persoonia pinifolia	terete, grooved above	31	31†	13·3	8·46	13·3	8·46	—	—
Persoonia salicina	broad lanceolate	20	20	12·5	2·03	12·5	2·03	33	4·61
Epacris microphylla	small, cordate-ovate	—	281	—	—	24·8	1·86	46	3·62
Lysinema pungens	cordate, tapering	—	312	—	—	19·9	2·24	40	3·48
Bossiaea scolopendria	cladode	114	114	10·6	1·01	10·6	1·01	—	—
Gompholobium latifolium	3 foliate, narrow	—	229	—	—	18·9	1·45	46	3·32
Platylobium formosum	ovate lanceolate	—	293	—	—	19·5	1·77	37	4·04
Pultenaea elliptica	elliptical-oblong	104	—	16·9	1·46	—	—	25	2·88
Pultenaea stipularis	narrow, linear	73	—	16·5	1·76	—	—	33	2·81
Angophora cordifolia	ovate, cordate base	—	—	—	—	—	—	34	4·61
Eucalyptus haemastoma	lanceolate	104	114	6·7	0·95	6·6	0·83	—	—
Leptospermum attenuatum	narrow lanceolate	281	187	11·6	1·26	9·3	2·10	—	—
Leptospermum flavescens	narrow oblong-obovate	140	146	10·4	2·45	11·9	1·73	—	—
Boronia pinnata	pinnate	(f)	187	—	—	23·2	2·13	23	2·28
Hemigenia purpurea	terete, grooved above	73	62†	14·3	1·24	13·0	1·36	—	—
Bauera rubioides	3 foliate, lanceolate	—	166	—	—	14·5	1·52	—	—
Helichrysum diosmifolium	narrow linear, recurved	—	—	—	—	—	—	23	3·21

Rain-Forest.

Lomatia Fraseri	narrow lanceolate	—	187	—	—	14·5	1·34	27	3·00
Trochocarpa laurina	ovate	—	187	—	—	14·9	3·17	29	3·79
Backhousia myrtifolia	ovate, acuminate	—	499	—	—	19·9	0·97	21	—
Eugenia Smithii	ovate, usually acuminate	—	281	—	—	9·7	0·94	17	3·06
Rhodamnia trinervia	ovate oblong, acuminate	—	510	—	—	14·9	0·62	28	0·22
Pittosporum undulatum	lanceolate	—	322	—	—	13·1	1·59	20	3·06
Doryphora sassafras	oblong lanceolate	—	94	—	—	7·7	0·94	21	2·78
Palmeria scandens	broadly elliptical	—	73	—	—	8·1	1·72	19	2·10

S.F.u = mean stomatal frequency per square millimetre (upper epidermis).
S.F.l = mean stomatal frequency per square millimetre (lower epidermis).
S.I.u = mean stomatal index (upper epidermis).
S.I.l = mean stomatal index (lower epidermis).
V.B. = percentage area occupied by vascular tissue (surface view).
σ = standard deviation from mean.
(f) = sometimes a few present.
† = two stomatal figures given as though the leaf were isobilateral.

TABLE 1.—*Continued.*

Plant.	Type of Leaf.		S.F.u.	S.F.*l.*	S.I.u.	σ Mean.	S.I.*l.*	σ Mean.	V.B.	σ Mean
Dodonaea triquetra	.. narrow lanceolate	..	—	198	—	—	15·0	1·84	30	2·24
Drimys insipida	.. oblong lanceolate	..	—	114	—	—	10·1	1·18	15	2·29
Claoxylon australe	.. oblong to oval, large	..	—	156	—	—	16·7	0·94	12	0·22
Sloanea australis ..	.. obovate-oblong, large	..	—	364	—	—	9·9	0·52	24	3·87
Synoum glandulosum	.. pinnate	..	—	83	—	—	6·4	1·23	13	1·00
Rhipogonum album	.. ovate, large ..	..	—	104	—	—	14·6	1·19	16	1·73
Ceratopetalum apetalum ..	lanceolate ..	..	—	375	—	—	10·8	1·39	29	2·90

S.F.u = mean stomatal frequency per square millimetre (upper epidermis).
S.F.*l* = mean stomatal frequency per square millimetre (lower epidermis).
S.I.u = mean stomatal index (upper epidermis).
S.I.*l* = mean stomatal index (lower epidermis).
V.B. = percentage area occupied by vascular tissue (surface view).
σ = standard deviation from mean.

TABLE 2.

Comparison of Average Stomatal Indices for various habitats.

Habitat.	Mean Stomatal Index.	σ Mean.	Source.
Aquatic and marsh (England)	10·62	6·78	Salisbury.
Woodland (England)	21·74	1·88	,,
Alpine and Arctic (England)	18·20	1·00	,,
Saltmarsh, sandstone, etc. (England)	21·68	6·72	,,
Sclerophyll forest, ridges and slopes (N.S.W.) ..	12·95	6·27	Carey.
Rain-forest (N.S.W.)	12·42	3·80	,,

Although the stomatal index is independent of the environment, as the above figures indicate, there is then a possibility that it may be characteristic of the family, or the genus. However, detailed examination of the figures shows no correlation between stomatal indices of the genera of any one family. Mostly they exhibit quite a wide range, as is shown in Table 3 below.

TABLE 3.

Range of Stomatal Indices in Families as shown by species examined.

Family.	Range of Stomatal Index.	Types.
Proteaceae	7·1–17·3	*Hakea gibbosa–Lomatia silaifolia.*
Epacridaceae	19·9–24·8	*Lysinema pungens–Epacris microphylla.*
Leguminosae	19·5–10·6	*Bossiaea scolopendria–Platylobium formosum.*
Myrtaceae	6·6–19·9	*Eucalyptus haemastoma–Leptospermum flavescens*

There remains then the possibility that this factor is a characteristic of the genus. It appears that there is no wide divergence between species, even those growing in markedly different environments. For example, the stomatal index of *Lomatia silaifolia* (sclerophyll type) is 17·3, while that of *Lomatia Fraseri* (rain-forest type) is 14·5. The closest similarity is shown between species of the same habitat as is seen in *Pultenaea*, where *P. elliptica* has a stomatal index of 16·9, and *P. stipularis* of 16·5. The number of species examined is not sufficient for one to be dogmatic on this point, but the present evidence seems to indicate that stomatal index is probably an hereditary character which fluctuates to some degree, some species being more plastic than others.

Vascular tissue of leaves.—An examination was made of the venation of the leaves, as it was considered that the number of the veins and the closeness of their mesh might be of extreme importance in the determination of the suitability of a species to a habitat (Zalenski, 1904). First, measurements were taken of the depth of the vascular bundles in relation to the thickness of the leaf, but as no consistent figures were obtained this was discontinued. It was observed, however, that there appeared to be a wider spacing of the bundles among the leaves of rain-forest types, e.g., *Claoxylon australe, Doryphora sassafras* (Text-figs. 5a, 5b), than among those of sclerophyll types, e.g., *Lomatia silaifolia, Bauera rubioides, Gompholobium latifolium* (Text-figs. 5c, 5d, 5e). Therefore, attention was concentrated on the arrangement of the veins as seen from above, and the percentage area of leaf-surface which they occupied. Ten counts were considered advisable in each species, being one from each of ten leaves, representing at least five plants. However, before the full number had been completed in each case the results seemed definite enough to conclude the investigation. The readings were determined from part of an area not more than one centimetre square, taken as near the middle of the leaf as is possible without including the midvein. These leaf segments were boiled in nitric acid, washed in water, and the epidermis and as
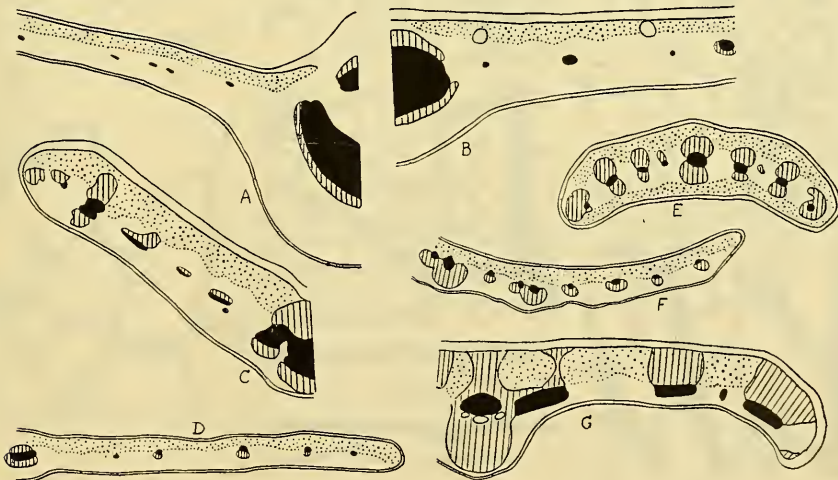
Text-figure 5.—Diagram of a transverse section of the leaf of: *a, Claoxylon australe*; *b, Doryphora sassafras*; *c, Lomatia silaifolia*; *d, Bauera rubioides*; *e, Gompholobium latifolium*; *f, Epacris microphylla*; *g, Lambertia formosa.* (× 25.) Black areas = Vascular tissue; Shaded areas = Fibres; Dotted areas = Palisade tissue.

much of the mesophyll as possible removed. It was obvious at once that this removal of mesophyll was much more readily accomplished in sclerophyllous types (excluding the Myrtaceae) than in rain-forest types. In the latter a sharp definition of the limit of the veins was difficult to attain. In this determination it was impossible to distinguish between bundle-sheath and conducting tissue in the sclerophyllous species, so that the figures given for the percentage of vascular tissue include the bundle-sheath. This gives a somewhat misleading impression as fibres are developed in all sclerophyllous types, being most numerous in the exposed species, e.g., *Gompholobium latifolium, Lomatia silaifolia, Isopogon*, etc. (Text-figs. 5*e*, 5*c*), and least in those growing further down the slopes, e.g., *Bauera rubioides* (Text-fig. 5*d*). In a few cases the fibres seem to spread laterally some little distance beyond the bundle, for instance, in *Epacris microphylla*, and *Lambertia formosa* (Text-figs. 5*f*, 5*g*) making its width in surface view much greater. In rain-forest plants, except for the midvein and sometimes a few other major veins, the sheath is parenchymatous.

However, camera lucida drawings were made of the venation in an area of 0·1156 square millimetre. Here again difficulty was experienced. Limitation of the area was necessary because decreased magnification and a larger area made the outline of the finer bundles uncertain and the results inaccurate. An outline
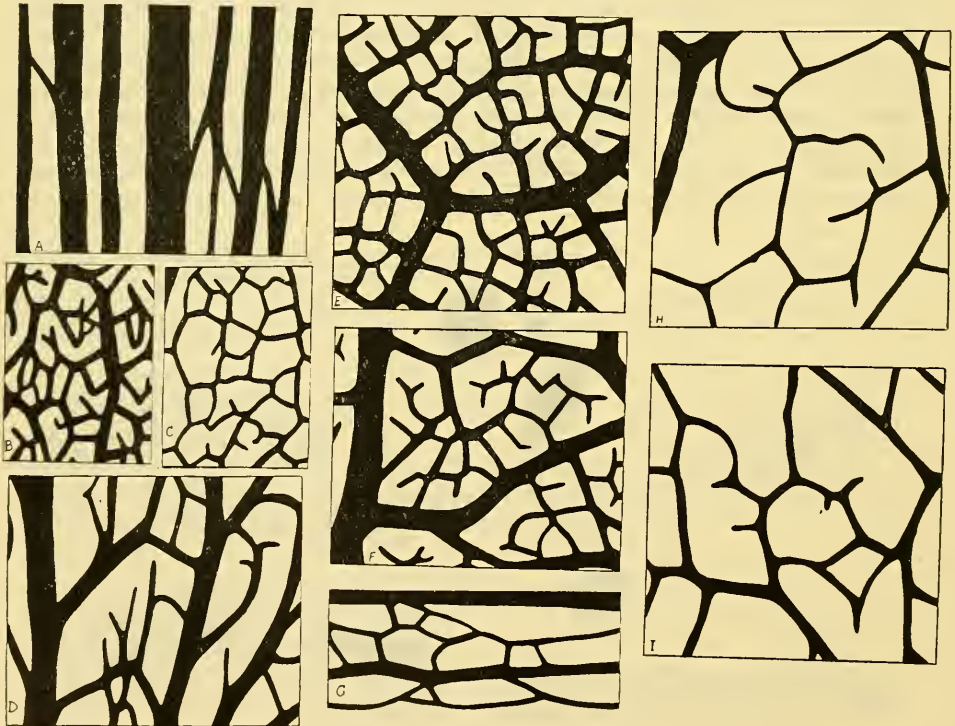
Text-figure 6.—Veins of leaves of the following plants, as seen in surface view: *a, Gompholobium latifolium*; *b, Banksia spinulosa*; *c, Helichrysum diosmifolium*; *d, Lysinema pungens*; *e, Angophora cordifolia*; *f, Platylobium formosum*; *g, Pultenaea stipularis*; *h, Drimys insipida*; *i, Doryphora sassafras.* (× 25.)

drawing on uniform paper was obtained, and then, by the process of cutting out and weighing, the percentage area occupied by the veins and their associated sheaths was determined. The average results for the individual species are listed in Table 1. In these determinations terete leaves and certain flat leaves in which it was thought that the results would be inaccurate, e.g., *Hakea saligna* (on account of the sclereids), were omitted.

Among the sclerophylls there is considerable variation in the type of venation. In leaves such as those of *Gompholobium latifolium* (Text-fig. 6a) and *Isopogon* the veins appear coarse, running almost parallel to one another, with here and there oblique veins linking them. In such cases the whole system is unbroken. On the other hand, the majority of the leaves have a more closely reticulate arrangement, with a number of short lateral vein-endings. In some types there is little variation in the diameter of the veins (*Banksia spinulosa* and *Helichrysum diosmifolium* (Text-figs. 6b, 6c)); while in other cases there is a number of well-defined lateral veins, their interstices occupied by finer bundles with a greater or less number of vein-endings, e.g., *Angophora cordifolia*, *Platylobium formosum*, *Lambertia formosa*, *Pultenaea stipularis* (Text-figs. 6e, 6f, 6g). In *Lysinema pungens* (Text-fig. 6d) and *Epacris microphylla*, there is a series of well-marked veins radiating from the leaf-base, between which are finer ramifications with a number of coarse vein-endings. In the rain-forest the venation is of the open reticulate type with a parenchymatous bundle-sheath, except in the case of the larger veins, e.g., *Drimys insipida*, *Doryphora sassafras* (Text-figs. 6h, 6i).

Table 1 shows the results of this investigation for the individual species. When these determinations are summarized (Table 4) it is found that, on the average, 37% of the leaf-area in the plants of sclerophyll forest is occupied by veins, and 21% in the plants of rain-forest.

TABLE 4.

Average percentage area of vascular tissue in leaves from various habitats.

Forest Type.	Mean Percentage Area Occupied by Veins.	σ Mean.
Sclerophyll forest of ridges and slopes	37	2·91
Rain-forest	21	6·17

Thus it is clear that there is a significant difference between the percentage of vascular tissue in the leaves of the xeric and mesic forest types. This is in accordance with the findings of Zalenski (1904), in that it indicates a parallelism between venation of a leaf and the water supply in the habitat.

SUMMARY.

1. A description is given of the anatomical variations shown in leaves taken from plants growing in sclerophyll forests and rain-forests.

2. The chief observations are those regarding stomata (in surface view and in section) and vascular tissue, as it was thought that these might show some noteworthy correlation with the habitat.

3. Tables are given of the stomatal indices of species from both environments, together with the standard deviations of their means. These are compared with the figures given by Salisbury for northern hemisphere types. They indicate

a significant difference between the mean stomatal indices of rain-forest types in England and New South Wales, but apart from this there is no relation between stomatal index and environment. The only indication of constancy in stomatal index is found among species of the same genus.

4. The percentage area of leaves, as seen in surface view, occupied by vascular tissue is tabulated. These figures show that sclerophylls exhibit a more closely reticulate venation than rain-forest types, which is in accordance with the experience of previous workers in the northern hemisphere.

My thanks are due to Professor T. G. B. Osborn, University of Oxford, for suggesting this investigation, and to Professor E. Ashby, University of Sydney, for his helpful criticism and advice in the preparation of this paper.

Literature Cited.

CANNON, W. A., 1924.—General and physiological features of the vegetation of the more arid portions of South Africa with notes on the climatic environment. *Carneg. Inst. Wash. Publ.* 354, pp. 77-110.

McLUCKIE, J., and PETRIE, A. H. K., 1927.—An ecological study of the flora of Mt. Wilson. Part iv. Habitat factors and plant response. PROC. LINN. SOC. N.S.W., lii, pt. ii, pp. 173-181.

MAXIMOV, N. A., 1929.—Plant in relation to water. Allen & Unwin, London, pp. 328-373.

SALISBURY, E. J., 1927.—On the causes and ecological significance of stomatal frequency, with special reference to Woodland flora. *Phil. Trans. Roy. Soc. London,* 216B, pp. 1-65.

WILSON, H. W., 1924.—Studies in the transpiration of some Australian plants, with notes on the structure of their leaves. *Proc. Roy. Soc. Victoria,* xxxvi, New Ser., Pt. ii, pp. 186-224.

WOOD, J. G., 1923.—On transpiration in the field of some plants from arid regions of South Australia, with notes on their physiological anatomy. *Trans. Roy. Soc. S. Aust.,* xlvii, pp. 259-78.

————, 1924.—The relations between distribution, structure and transpiration of arid South Australian plants. *Trans. Roy. Soc. S. Aust.,* xlviii, pp. 226-35.

————, 1934.—Physiology of xerophytism in Australian plants. The stomatal frequencies, transpiration, osmotic pressures of sclerophyll and tomentose succulent leaved plants. *Journ. Ecol.,* xxii, No. 1, pp. 69-85.

ZALENSKI, V., 1904.—Materials for the study of the quantitative anatomy of different leaves of the same plant. *Mém. Polytech. Inst. Kiev.,* iv, pp. 1-203 (in Russian).